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October, 1954

MADROÑO

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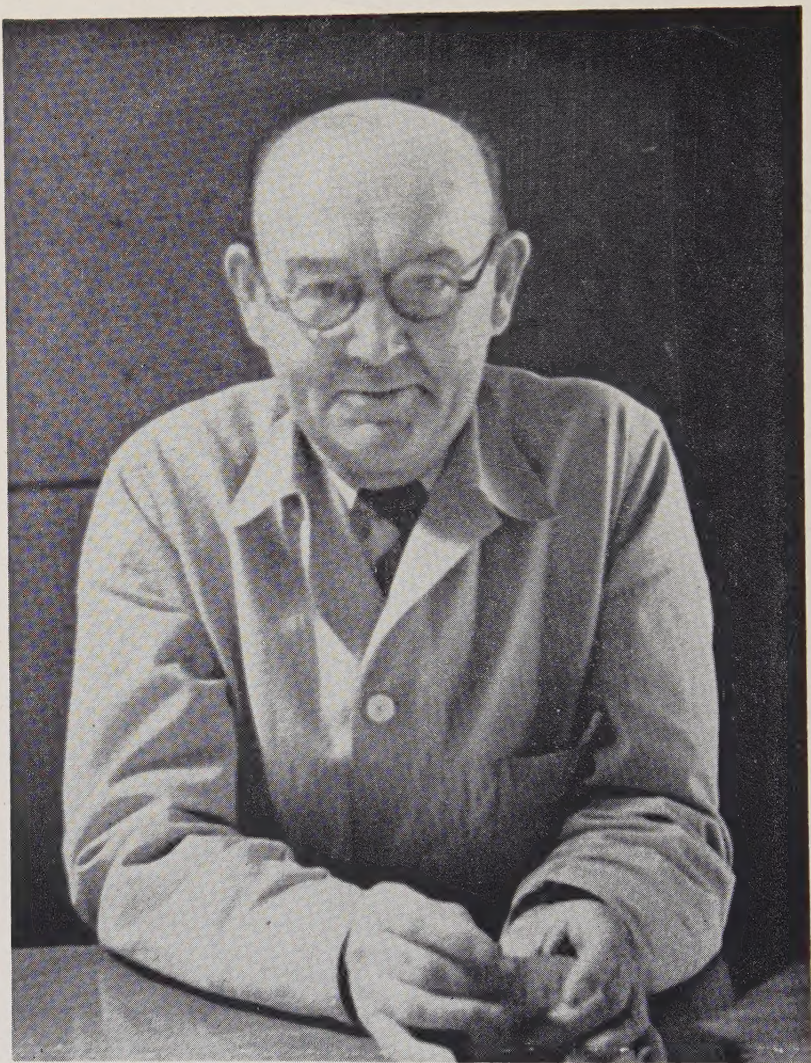
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LEROY ABRAMS
(Emeritus Professor of Botany, Stanford University)

LEROY ABRAMS

A TRIBUTE FROM THE CALIFORNIA BOTANICAL SOCIETY

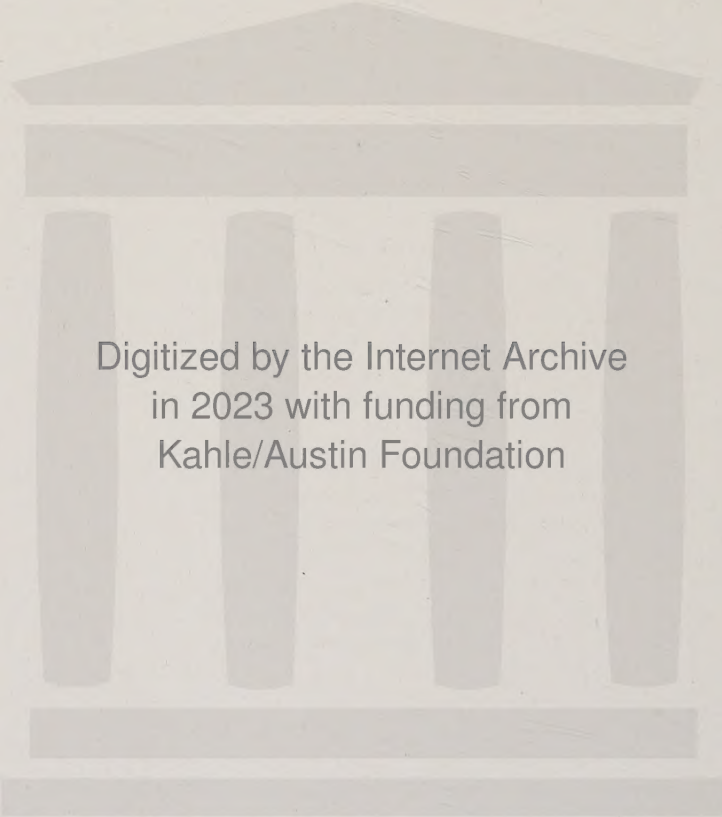
October 1, 1954

On the occasion of this, your eightieth birthday, we of the California Botanical Society take the opportunity to congratulate you on your success as an individual, as a model teacher, research worker, and as an outstanding contributor to our knowledge of the native flora of the Pacific States, and we wish for you and Mrs. Abrams continued health and contentment.

Your childhood in Iowa, your boyhood, first in Oregon and later in Southern California, your schoolday friendship with the late Harvey Monroe Hall, your student days at Stanford where you worked with Campbell and Dudley with a primary interest in cryptogamic botany, your acting professorship, upon graduation in 1899, for a year at the University of Idaho, your return to Stanford to take up an assistantship, your fellowship at the New York Botanical Garden where you came in contact with Britton, your associations on the staff of the National Herbarium with Maxon and Coville, and finally your return again to Stanford, first to assist Professor Dudley and then to succeed him—this series of associations has contributed to the breadth of background that peculiarly qualified you so successfully to undertake your *magnum opus* and lasting monument, "An Illustrated Flora of the Pacific States."

Your friendly informal approach with your students has prompted a reciprocal attitude and has resulted in an impact that has led them to recall your very words and manner of expression in retrospect when in later associations points have been raised—be they matters of botanical lore, plant geography or fact of taxonomy. Your kindness and complete absence of pettiness have won their affection and admiration. You have shown an innate capacity for inspiring devotion in your students and associates. No better example can be cited than the able and devoted editorship of Mrs. Ferris in bringing the final volume of the "Flora" to completion. Your students regard the opportunity to have worked with you as their very rare good fortune.

Again, we salute you and Mrs. Abrams and wish for you more years of serenity and happiness in your ever attractive hilltop home on the Stanford Campus.—R. C. B., H. L. M.



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MORPHOLOGICAL AND ECOLOGICAL CONSIDERATIONS IN
THE CLASSIFICATION OF NAVARRETIA (POLEMONIACEAE)

BEECHER CRAMPTON

Ruiz and Pavon (1799) erected the genus *Navarretia* upon *N. involucrata*, the only species of the genus occurring in South America. Mason (1951) recognizes twenty-nine species of the genus occurring in Western North America and centering chiefly in California. It is the purpose of this paper to examine more closely some of the morphological and ecological features of these species as an aid to increased understanding of their interrelationships. All species were studied from herbarium specimens at the University of California at Berkeley, the author's collections, and in some instances cultivated material. Specific reference to any particular plant material has been made only when exceptional variations are worthy of note or limited material warrants citation.

MORPHOLOGICAL CRITERIA

The possible evolutionary significance of several morphological features, mainly floral, became evident during this investigation. Among these, corolla venation, stamen insertion, stigma lobing, capsule modifications, seed number, glands, and vessel anatomy, will be discussed in turn.

1. COROLLA VENATION

The vascular supply to the corolla may be readily observed. Flowers from herbarium specimens or living plants are allowed to become fully soaked in water on a glass slide, a very simple process which is sufficient for clearing, and adequate to reveal the vascular system. The use of a dark background on a binocular dissecting microscope and careful longitudinal slitting of the corolla tube exposes the complete vasculature pattern and clearly shows the position of stamens and style. Stamen vasculature is similar throughout the genus, the stamens always being supplied by single veins which alternate with the petal veins. Inasmuch as significant variation is lacking, stamen vasculature is omitted in the following discussion.

Corolla vasculature, other than that supplying the stamens, has been found, however, to be of significance. With the exception of the South American *N. involucrata*, *Navarretia* may be divided into those species having trinervate vasculature and those having uninervate vasculature of the corollas. Twenty-one species fall into the trinervate group wherein a single vein for each lobe enters the base of the corolla tube and almost immediately branches into three veins which traverse the tube and enter the lobe unfused (fig. 1). The number of veinlets and degree of their fusion in the corolla lobe is of secondary importance and will not be considered.

Navarretia subuligera deviates from the typical trinervate condition. In this species, the vein to the corolla lobe branches about one-third of the way up the corolla tube and enters the lobe unfused (fig. 2). This modification of the typical trinervate condition is of interest when compared with the vasculature of the remaining eight species.

The second series of plants comprising eight species shows a vascular pattern with a single vein traversing the corolla from the base of the tube to the lobe. Plants in this series will be referred to as uninervate. The single vein entering the corolla lobe becomes variously branched or remains unbranched, depending upon the species (figs. 3, 4, 5). The consistency with which such patterns occur within a single species or several merits attention developmentally and taxonomically.

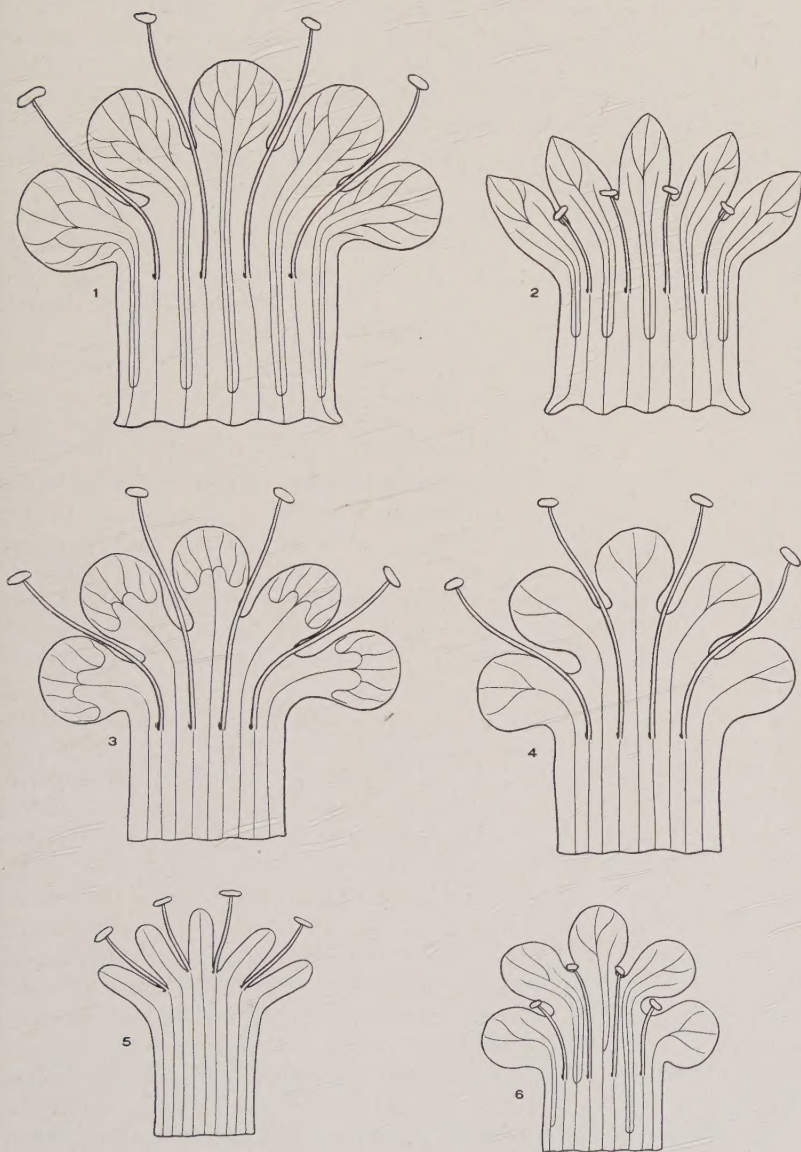
Among these uninervate species, *N. intertexta* retains a terminal corolla lobe pattern which is comparable to that of the trinervate species (fig. 3), a pattern which may be used to distinguish it from the closely related *N. propinqua* (fig. 4), wherein the two or three terminal veinlets in the corolla lobe are disposed divaricately. *Navarretia leucocephala* shows a similar pattern, but differs from *N. propinqua* in shape of the apex of the calyx membrane, stamen insertion, stigma lobing, and habitat. The remaining species in the uninervate series, *N. prostrata*, *N. minima*, *N. bakeri*, *N. plieantha*, and *N. pauciflora*, have a single unbranched vein traversing the entire corolla, from the base to the summit of the lobe and represent the ultimate reduction in corolla vasculature in the genus (fig. 5).

The only South American species, *N. involucrata*, although related to the uninervate series, is treated separately because of its exceptional and distinctive vasculature. Whereas the twenty-nine species of western North America are consistently either trinervate or uninervate, with no variations between these patterns, all Chilean collections of *N. involucrata* examined (*Morrison & Wagenknecht* 17122, *C. & G. Grandjot* 3981, 3642, 1065, *A. Donat* 285) showed variable reduction in vasculature within individual corollas on the same plant (fig. 6). This may be a consistent feature of this isolated species, and indicates an obvious specialization of vasculature directed towards the uninervate pattern from the trinervate.

2. STAMEN INSERTION

The concept of sympetalous corollas and epipetalous stamens involves a fusion of tissue of petals and staminal filaments to form the corolla tube and throat; from this tissue projects the unfused remainder of the anther-bearing filament. A remarkable series of positions of stamen insertion is evident in *Navarretia*, the different positions being definitely correlated with other structural features of the corolla.

In *N. mellita* the stamens are inserted nearly at the base of the corolla tube, leaving an exceptional long throat above (fig. 7). *Navarretia squarrosa*, a closely related species, shows the stamens to be inserted about or shortly below the middle of the corolla tube (fig. 8). In this regard, these



FIGS. 1-6. Types of corolla vasculature in *Navarretia*. FIG. 1. *N. mitracarpa* showing trinervate vasculature typical of the section *Eunavarretia* (corollas 7.5 mm. long). FIG. 2. *N. subuligera* (corollas 5.5 mm. long). FIG. 3. *N. intertexta* (corollas 6 mm. long). FIG. 4. *N. propinqua* (corollas 6 mm. long). FIG. 5. *N. plieantha* (corollas 5 mm. long). FIG. 6. *N. involucreta*, vascular pattern believed to be typical of this species (corollas 4 mm. long). The fifth stamen and its trace are not shown. Illustrations are semidiagrammatic.

two species are significant since they exhibit the lowest position of stamen insertion in any *Navarretia* corolla. A typical stamen insertion is exemplified by *N. pubescens* (fig. 9). For the most part, however, staminal insertion ranges from slightly above the middle of the corolla tube up to the sinuses of the corolla lobes. An evident correlation exists between the amount of corolla vasculature and the point of stamen insertion. The trinervate species generally have stamens inserted from near the base to about the middle of the corolla throat, except for those species which have unequal insertion with one or two stamens in the upper half of the throat. In the uninervate species, except for *N. intertexta* and *N. propinqua*, stamens are inserted above the middle of the corolla throat to the sinuses of the corolla lobes. All the uninervate species with a single unbranched vein supplying each corolla lobe have stamens inserted in or immediately below the sinuses of the corolla lobes (figs. 5, 10).

On the basis of this evidence it is concluded that there has been a definite migration of stamen insertion from near the base of the corolla to the very summit of the corolla tube, a migration correlated with progressive reduction of vasculature within the corolla.

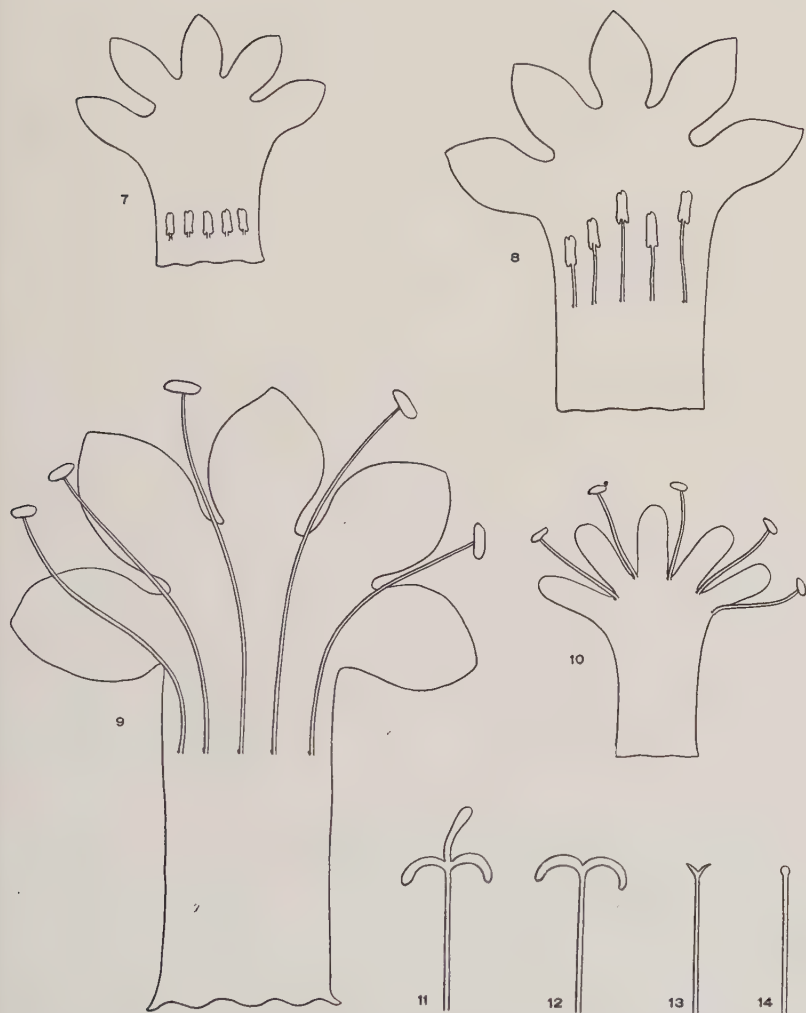
3. STIGMA LOBING

In all trinervate species the stigmas are prominently 2- or 3-cleft (figs. 11, 12). Three-cleft stigmas are found in those species with 3-locular capsules, while 2-cleft stigmas occur with 1-2-locular capsules. The uninervate species with indehiscent capsules usually have minutely 2-lobed or entire stigmas (figs. 13, 14). Two exceptions, *N. intertexta* and *N. propinqua* retain a prominently 2-cleft stigma reminiscent of the trinervate species. Developmentally, the stigma has become modified from a deeply 3-cleft condition to one of entirety in coordination with capsular modification, and seemingly along with progressive reduction in corolla vasculature which is particularly evident in the uninervate species.

4. CAPSULE MODIFICATION

Greene (1887) remarked: "The astonishing range of variability in the capsule of *Navarretia* which will be brought to view in classification and description of species is almost something new in kind, in the annals of carpology, I think." Unquestionably capsule structure and behavior are highly important for classification and in understanding species interrelationships.

Two distinct phases of capsular structure and dehiscence are characteristic of *Navarretia*. The majority of the species have coriaceous, or chartaceous, dehiscent capsules, while the remainder are membranous, weak-walled, and indehiscent. The species with dehiscent capsules exhibit a variety of texture, structure, manner of opening, and except for *N. tagetina* and *N. subuligera*, release their seeds as discrete units. Four species, *N. squarrosa*, *N. mellita*, *N. heterodoxa* and *N. peninsularis*, have 3-celled coriaceous capsules which, upon dehiscence, split into three valves that



FIGS. 7-10. Types of stamen insertion in *Navarretia*. FIG. 7. *N. mellita*, note extremely short filaments; anthers are versatile (corollas 5 mm. long). FIG. 8. *N. squarrosa*, note filaments are longer than the anthers; anthers are versatile (corollas 10 mm. long). FIG. 9. *N. pubescens*, showing type of stamen insertion generally typical of section *Eunavarretia* (corollas 16 mm. long). FIG. 10. *N. bakeri*, stamen insertion in the sinuses of the corolla lobes (corollas 5 mm. long). FIGS. 11-14. Types of stigma lobing in *Navarretia*. FIGS. 11-12. Stigmas typical of the section *Eunavarretia*. FIGS. 13, 14. Stigmas typical of the section *Fragiles*. Illustrations are semi-diagrammatic.

separate from the top downwards, usually remain united at the base, and release six or more seeds from each locule. Six species, *N. hamata*, *N. atractyloides*, *N. viscidula*, *N. breweri*, *N. prolifera* and *N. divaricata*, possess 3-celled, coriaceous capsules that separate into discrete valves from the

base upwards, and release three to five seeds per locule. *Navarretia filicaulis* has become modified into a 2-celled, chartaceous capsule which splits, upon dehiscence, into two discrete valves, freeing 6 to 8 seeds. Six species, *N. pubescens*, *N. mitracarpa*, *N. jepsonii*; *N. heterandra*, *N. eriocephala* and *N. cotulaefolia*, are modified in another direction. The capsules disintegrate about the base, leaving a chartaceous "cap" enveloping the seeds. All are unilocular, 1-seeded, except for *N. pubescens*, which may also be 2-seeded and represent culmination in reduction of number of locules and number of seeds. The capsule of *N. nigellaeformis* is further modified by disintegration of the lower third, but remains 2-celled and releases 4 to 5 seeds. *Navarretia setiloba* capsules dehisce about the middle, are 1-celled and 1-seeded. This trend in progressive capsule disintegration culminates in two species, *N. tagetina* and *N. subuligera*. *Navarretia tagetina* retains a small chartaceous cap at the summit of the capsule; the remainder disintegrates and releases several coherent seeds. *Navarretia subuligera* is wholly membranous and does not regularly dehisce, but disintegrates leaving 3 or 4 coherent seeds. These two species retain three locules, even though the locule walls are thin; they also have the 3-cleft stigma.

With the exception then, of *N. tagetina* and *N. subuligera*, the weak-walled, membranous, indehiscent capsule is characteristic of those plants with uninervate corollas and forms the second biological type in *Navarretia*. The capsules of this type disintegrate at maturity releasing seeds as a slightly coherent unit in contrast to the regularly dehiscent type discussed above. While most of the species in this type are unilocular and several seeded, *N. leucocephala* and *N. prostrata* are many-seeded and possess a somewhat imperfectly 2-locular capsule. Occasionally, *N. pauciflora* may have a 1-seeded capsule.

It is concluded, in the light of the foregoing criteria, as well as evidence from the capsule, that the primitive capsule of *Navarretia* was 3-locular, coriaceous, and separated upon dehiscence into discrete valves releasing numerous seeds. A modification in structure and texture produced a 2-locular, chartaceous capsule. This, in turn, culminated in a capsule that is unilocular and 1-seeded with a papery or chartaceous envelope that disintegrates about the base upon dehiscence. *N. tagetina* and *N. subuligera* become transitional between regular dehiscence in the trinervate species and indehiscence in the advanced uninervate species.

5. SEED NUMBER

Navarretia squarrosa, with 6 to 9 seeds per locule, has the largest number of seeds of any species. Seed number becomes progressively reduced, depending upon capsular modifications, and culminates in seven unilocular, 1-seeded species already mentioned. *Navarretia pubescens*, a member of this group, matures 1- and 2-seeded capsules within the same flowering head, but those with one seed are in the majority. As already discussed the trinervate species possessing regularly dehiscent capsules exhibit wide

variation between species as to the number of ovules matured. The indehiscent capsule of the uninervate species has a narrower range of seeds produced. *Navarretia leucocephala* and *N. prostrata* are many-seeded, probably 8 to 10 seeds per capsule, *N. minima* and *N. bakeri* are 4 to 5-seeded, *N. plieantha* is 2-4-seeded, and *N. pauciflora* is 1-4-seeded. *Navarretia intertexta* and *N. propinqua* are variable in the number of seeds usually maturing, about 4 to 8 per capsule. *Navarretia pauciflora* represents the culmination of reduction in seed number in this series of plants.

6. GLANDS

Along with other morphological criteria being considered, the prevalence of glands among *Navarretia* species appears to have important evolutionary significance. Unquestionably the heaviest concentration of glands upon the foliar and floral parts occurs in the trinervate species, *N. squarrosa*, *N. atractylodes*, *N. hamata*, *N. viscidula*, *N. mellita* and *N. heterodoxa*. The first four species are characterized by their strong mephitic odor, while the latter two are honey-scented and citrus-scented respectively. Glandular development decreases throughout the trinervate species and terminates with *N. subuligera* which is practically glabrous throughout. In this species a few scattered glands occur about the abaxial base of the bracts in the flowering heads. This glandless condition becomes very prevalent in the uninervate species which develop glands only on the abaxial base of the bracts and the calyx lobes. In some instances uninervate species may be entirely devoid of glands. It is apparent that a decrease in development of glands has to some extent followed progressive specialization of other plant structures and changes in habitat.

7. VESSEL ANATOMY

Stems from all species of *Navarretia* were macerated, and cleaned sections immersed from 6 to 12 hours, at room temperature, in a 10 per cent solution of nitric and chromic acids. The macerated wood was then stained with safranin in 50 per cent alcohol, passed through 50-100 per cent alcohol series, and permanently mounted in diaphane.

Examination of all species revealed some variation in vessel length and breadth. *Navarretia propinqua* has vessel elements averaging nearly 0.8 mm. in length and 0.019 mm. in width, by far the longest vessels found in any species, the closest rival being *N. involucrata* with an average of 0.7 mm. in length. The average and usual length of vessels in *Navarretia* is between 0.4 and 0.5 mm., the shortest being 0.25 in *N. tagetina*. All species have vessels with porous perforation plates. In *N. squarrosa*, however, both reticulate and scalariform¹ perforation plates commonly occur. There is some evidence that this condition may occur regularly in *N. atractylodes*, since several mounts of this species had a few vessels with scalariform perforation plates. Studies of anatomy by I. W. Bailey and his co-workers have indicated that scalariform and reticulate perforation

¹ Two to six bars are found in perforation plates of this type.

plates in vessels are more primitive than the derived porous condition. If this consideration is applied here in conjunction with evidence from other criteria, *N. squarrosa* is indicated as the most primitive species in the genus *Navarretia*.

ECOLOGICAL CONSIDERATIONS

Two distinct groups of species may be recognized on the basis of ecological preference. The majority of species is found over a wide range of habitats which includes open plains, valley, meadow, or hillside, while a minority is confined in whole or part to vernal pools.

1. VARIED HABITAT.

Navarretia squarrosa ranges extensively along the Pacific Coast, rarely occurring very far inland, and particularly favoring cultivated or disturbed soil. It behaves as a ruderal in grain and other fields and along roadsides, but it is not rare to find stands of this species in hard-packed undisturbed soil. There is a tendency for the majority of these plants to be aggregated in areas with small pockets or depressions where water has stood during the spring. *Navarretia squarrosa* is remarkable for its long period of flowering, so that frequently on a single plant capsules ripen and dehisce while young heads continue to appear and flower. The long duration of anthesis from June to November, coupled with remarkable powers of rejuvenation following heavy injury, carries a suggestion of perennial behavior.

Navarretia mellita, a closely related species, occurs farther inland along the inner Coast Ranges of California, reaching its greatest development in association with chaparral. Frequently, however, it is found in disturbed soil along roadsides and occasionally on serpentine soils but never becomes weedy as does *N. squarrosa*.

Navarretia mitracarpa extends spottily from southern Oregon, through the inner Coast Ranges of California, to Santa Barbara County, reaching its greatest abundance in Monterey and San Luis Obispo counties. It reportedly occurs on serpentine soils, but whether exclusively or not requires further investigation. *Navarretia jepsonii* is especially partial to serpentine soil although it is not wholly restricted to it. Its range of distribution is from northern Napa County, California, into southern Lake County and east into western Colusa County. Most plants of *N. mitracarpa* and *N. jepsonii* appear to develop conspicuous reddish foliage and stems when found on serpentine. *Navarretia cotulaefolia* prefers meadow or even marshy conditions, occurring through the inner Coast Ranges of California and extending into the Sacramento Valley. *Navarretia divaricata* favors open pine forests and occurs in Idaho, southern Oregon, the mountains of the northern Coast Ranges of California, the Sierra Nevada, and in Santa Barbara County of California, at elevations of 4500–8000 feet. *Navarretia divaricata* subsp. *vividior* occurs from 1500–4000 feet in the northern Coast Ranges, Siskiyou and Modoc counties and south along the western slope of the Sierra Nevada to Mariposa County, and occupies

chaparral areas, roadsides, and open flats. *Navarretia breweri* prefers elevations of 5000–8000 feet, in open valleys, flats or meadows on the eastern slopes of the Cascades and Sierra Nevada mountains and extends generally throughout the Great Basin. Both *N. divaricata* and *N. breweri* are the only truly montane trinervate species and occur consistently above 4500 feet.

Navarretia setiloba is apparently restricted to the red clay soils in the vicinity of Haviilah and Kernville, Kern County, in the southern Sierra Nevada in California. *Navarretia subuligera*, a comparatively rare species, appears to be endemic upon rocky, volcanic soils in the north Coast Ranges and in the northern Sierra Nevada of California, judging from the limited material and data available. This restriction to the specialized habitat of volcanic soils agrees with other marks of specialization shown by this highly advanced species.

Most of the species occurring on open plains and hillsides appear to be tolerant of edaphic variables and show no apparent preferences. Very often two or more species of *Navarretia* are found growing interspersed in similar situations in a relatively small area. H. L. Mason (oral communication) reports that eight distinct species are found growing together in a meadow in southern Lake County, California. *Navarretia intertexta* and *N. propinqua* are the only two species of the uninervate series which occur in varied habitats; all other species are trinervate.

2. THE VERNAL POOL HABITAT.

The vernal pool habitat represents a major ecological specialization in *Navarretia*. Vernal pools range from small depressions in open plains, fields or valleys, to large swales that become filled with rain water in winter or early spring. Water gradually evaporates leaving either very hard packed soil, or, if the pools are very large, organic debris or peaty soil. Recession of the standing water encourages development of a flora whose members start development aquatically or in the muddy soil which later becomes hard and baked. Probably seeds of such *Navarretia* species germinate while still covered with water. *Navarretia leucocephala*, a common species in vernal pools of the Great Valley of California usually is found at the lowest point of the depression, suggesting aquatic germination; anthesis is reached before the soil has yet dried.

Six species, *N. bakeri*, *N. pauciflora*, *N. plieantha*, *N. prostrata*, *N. minima* and *N. leucocephala*, are confined almost exclusively to the vernal pool situations. Not only are these species very specialized ecologically, they are also all highly specialized morphologically having uninervate corollas, indehiscent capsules, entire or minutely 2-lobed stigmas, high stamen insertion and a paucity of glands. Peculiarities inherent to the vernal pool habitat may have influenced the development of an indehiscent capsule and reduction in glandulosity. The agglutinated seeds shed from the distintegrating capsule do not facilitate wide dispersal but this is not necessary in a limited habitat. The free seeds released by the de-

hiscent capsules of species in varied habitats insure dispersal over a wider area.

Glands, which probably restrict water loss to some degree, cease to be of value in a habitat which provides and holds within the soil sufficient water for the plant's demands regardless of loss through transpiration.

Navarretia intertexta, with indehiscent capsules and uninervate corollas, is basically allied to the vernal pool species. Ecologically, the species is exceptional in its wide tolerance of diversified habitats. It may be found on the edges of vernal pools, but is usually not an integral part of the vernal pool flora. More commonly it occurs on grassy plains, hillsides, meadows, dry creek beds or banks, roadsides, and even on serpentine soil. This is by far the most common species of *Navarretia*, having a wide range of distribution in California, Oregon, Washington, and Idaho. It frequently grows in association with other species, particularly *N. tagetina* and *N. pubescens*. While uninervate corolla, indehiscent capsule, and close association with the vernal pool habitat ally it with the uninervate series, the singular pattern of corolla lobe venation (fig. 3), the prominently 2-cleft stigma, the low stamen insertion, and the occurrence in varied habitats relate it to the larger trinervate series of species.

Navarretia propinqua, closely related to *N. intertexta* and often confused with it, occupies open plains, valleys, plateaus, and probably the edges of vernal pools. Principally a Great Basin species, it is found only east of the crest of the Cascade Mountains and the Sierra Nevada, where it has broad distribution in eastern Oregon, Washington, Idaho, Nevada, Utah, Colorado, and northern Arizona. *Navarretia intertexta* frequently occurs with it along the western and northern fringe of the Great Basin. The primary distinction between the two species is the pattern of corolla lobe venation (compare figs. 3 and 4).

The South American *N. involucrata* apparently occupies and is probably confined to vernal pools throughout the Andean Cordillera of Chile. One collection (*Morrison & Wagenknecht* 17, 122) refers to the species as growing, "in a small bog or vega, nearly dry." The indehiscent capsule and the specialized habitat link the species with the vernal pool group of western North America. However, the specialization in corolla vasculature (fig. 6), the 2-cleft stigma, and low stamen insertion mark the species as somewhat transitional between uninervate and trinervate groups.

CONCLUSIONS

Morphological and ecological evidence indicate two distinct developmental lines in the genus *Navarretia*. Two groups of species have been distinguished in *Navarretia* on the basis of corolla vasculature referred to as trinervate and uninervate, respectively. Other morphological and ecological features confirm separation of these two distinct developmental lines within the genus. It remains to assign sectional divisions to the genus. Brand (1907) first used the section *Eunavarretia*, which has been found to include many species with trinervate corollas, deep 2- or 3-cleft stig-

mas, low stamen insertion, and variable ecology. The sectional name *Eunavarretia* is thus appropriate for those species having these features. For the remaining nine species with uninervate corollas, indehiscent capsules, entire to 2-lobed stigmas, and shallow stamen insertion, which are generally confined to vernal pools, I propose a new sectional name.

NAVARRETIA, sect. **Fragiles** sect. nov. Corollae lobi univenosi capsula membranacea irregulariter dehiscens stigma 2-scissum vel 2-lobatum vel integrum flores caerulei vel albi; plantae stagnis vernalibus restrictae. The species in this group are a somewhat homogeneous group of similar habitat and general superficial appearance, but closer morphological examination reveals significant differences. These differences are largely biological, each species showing advanced structural modifications over the older and well delineated species of *Eunavarretia*.

Three species are of unusual interest since they show evidence of transition between the two sections. Corolla vasculature, capsule dehiscence, and specialized habitat place *N. subuligera* intermediate between the *Fragiles* and *Eunavarretia*. *Navarretia intertexta*, on the basis of corolla vasculature, 2-cleft stigma, stamen insertion, and wide range of ecological preference is closer to *Eunavarretia*. *Navarretia involucreta* is perhaps the most unique of these transitional species since corolla vasculature alternates between uninervate and trinervate.

The most highly specialized species in the genus is *N. pauciflora*, a position it holds by virtue of its morphological reduction and its restriction to a vernal pool habitat. *Navarretia squarrosa* appears to be the most primitive member because of its almost perennial behavior, large seed number, and the nature of the vessels.

Much of the taxonomic confusion in *Navarretia* has been cleared up by Mason (1951) and his descriptions and key merit close attention in unravelling interrelationships within the genus. On the basis of the criteria discussed in this paper, an attempt has been made to further clarify these relationships and call attention to the evidence derived from various means of attack. The key presented here emphasizes these features and attempts to group the species according to their degree of specialization.

KEY TO THE SECTIONS AND SPECIES OF NAVARRETIA

- A. Corolla lobes 1-veined; capsules membranous, indehiscent; stigmas entire, minutely 2-lobed, or 2-cleft; flowers pale blue or white; plants largely of vernal pools. Section 1. **FRAGILES**
- B. Stigmas entire or minutely 2-lobed; stamens inserted at mid-throat or above; calyx sinus-membrane truncate at summit; plants restricted to vernal pools.
- C. Single vein in the corolla lobes unbranched; corolla lobes linear.
- D. Stamens inserted in or immediately below the sinuses of the corolla lobes; flowers pale blue, rarely white.
- E. Corolla exceeding the longest calyx lobes.
- F. Plants erect, stems slender and branching from the base; heads few-flowered; stamens inserted immediately below the sinuses of the corolla lobes.
 - 1. *N. pauciflora* Mason

- FF. Plants prostrate, stems stoutish, proliferating from beneath a terminal head; heads many flowered; stamens inserted in the sinuses of the corolla lobes. 2. *N. prostrata* (Gray) Greene
- EE. Corolla shorter than the longest calyx lobes.
- G. Style slender, stigma 2-lobed, mature calyx with lobes nearly equal. 3. *N. pliantha* Mason
- GG. Style stoutish, stigma entire to minutely 2-lobed; mature calyx with one lobe conspicuously longer than the others. 4. *N. bakeri* Mason
- DD. Stamens inserted at mid-throat; flowers white. 5. *N. minima* Nutt.
- CC. Single vein in the corolla lobes divaricately branched; corolla lobes ovate.
- H. California 6. *N. leucocephala* Benth.
- HH. South America 7. *N. involucrata* R. & P.
- BB. Stigmas prominently 2-cleft; stamens inserted near the base of corolla throat; calyx sinus-membrane v-shaped at the summit; plants often bordering vernal pools but also in many diverse habitats.
- I. Single vein of the corolla lobes divaricately branched into 2-3 veinlets; corollas usually subequalling calyx lobes. 8. *N. propinqua* Suksd.
- II. Single vein of corolla lobes branched into 4-8 veinlets; corollas usually exceeding calyx lobes. 9. *N. intertexta* (Benth.) Hook.
- AA. Corolla lobes 3-veined; capsules coriaceous or chartaceous, dehiscent, rarely indehiscent; stigmas prominently 2- or 3-cleft; stamens usually inserted at mid-throat or below; flowers blue, violet, pink, or yellow; plants of open plains, valleys, meadows, or hillsides. Section 2. EUNAVARRETTIA
- J. Capsules not regularly dehiscent; stigmas 3-cleft, included; calyx with 2 very long and 3 very short lobes.
- K. Bracts and calyx lobes almost glabrous; stamens included; flowers cream white. 10. *N. subuligera* Greene
- KK. Bracts and calyx lobes coarsely villous; stamens exserted; flowers pale blue. 11. *N. tagetina* Greene
- JJ. Capsules regularly dehiscent by valves; stigmas 2- or 3-cleft, included or exserted; calyx lobes variously unequal.
- L. Capsules chartaceous, unilocular (rarely 2-locular); 1- 2-seeded; stigmas 2-cleft.
- M. Capsules circumscissile near the base.
- N. Corolla usually 4-merous.
- O. Heads coarsely villous; stamens equally inserted just below the sinuses of corolla lobes; flowers yellow or cream colored. 12. *N. cotulaefolia* (Benth.) H. & A.
- OO. Heads densely soft white-villous; stamens unequally inserted in throat; flowers blue or white. 13. *N. heterandra* Mason
- NN. Corolla regularly 5-merous.
- P. Capsules 4-valved; bract rachis expanded above or below.
- Q. Corollas yellow or cream-colored, often with purple spots; bract rachis expanded below. 14. *N. eriocephala* Mason
- QQ. Corollas purple, without purple spots; bract rachis expanded above.
- R. Capsules 1- or 2-seeded, chartaceous throughout. 15. *N. pubescens* (Benth.) Hook.
- RR. Capsules 1-seeded, thickened above along the sutures. 16. *N. mitracarpa* Greene
- PP. Capsules 8-valved; bract rachis linear throughout. 17. *N. jepsonii* Bailey

- MM. Capsules circumscissile at about the middle.
 S. Capsules 1-seeded; flowers purple. 18. *N. setiloba* Coville
 SS. Capsules 4-5 seeded; flowers yellow with purple spots. 19. *N. nigellaeformis* Greene
 MMM. Capsules not circumscissile, incompletely 2-locular, separating into two halves upon dehiscence. 20. *N. filicaulis* (Torr.) Greene
 LL. Capsules coriaceous, 3-locular, few to many-seeded; stigmas 3- cleft.
 T. Capsules few-seeded, dehiscent from the base upwards.
 U. Bracts palmate; branches proliferating from beneath terminal heads.
 V. Plants coarsely villous; flowers to 1 cm. long, purple or yellow; stamens exerted. 21. *N. prolifera* Greene
 VV. Plants glandular-puberulent; flowers up to 0.5 cm. long, pinkish; stamens included. 22. *N. divaricata* (Torr.) Greene
 UU. Bracts pinnate-filiform throughout; branches basal or cauline. 23. *N. breweri* (Gray) Greene
 UUU. Bracts expanded below, linear or lanceolate above. 24. *N. viscidula* Benth.
 UUUU. Bracts broad-ovate below with terminal segments of 3 divergent, pungent lobes.
 W. Stamens unequally inserted in throat; stigma included. 25. *N. attractyloides* (Benth.) H. & A.
 WW. Stamens equally inserted in throat; stigma exerted. 26. *N. hamata* Greene
 TT. Capsules many-seeded, dehiscent from the top downwards.
 X. Corolla tube persistent, ruptured on one side by the maturing capsule. 27. *N. peninsularis* Greene
 XX. Corolla tube circumscissile about the base and pushed upwards by the maturing capsule.
 Y. Bracts broadly ovate, at the base, digitately lobed above. 28. *N. heterodoxa* Greene
 YY. Bracts narrow and often crowded at the base with many unequal acerose lobes.
 Z. Plants slender, usually much branched; flowers pinkish; filaments shorter than the anthers and inserted near the base of the tube. 29. *N. mellita* Greene
 ZZ. Plants coarse, usually little-branched; flowers blue-violet; filaments longer than the anthers and inserted near mid-tube. 30. *N. squarrosa* (Eschsch.) H. & A.

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SUMMARY

1. Corolla venation is of two types, trinervate and uninervate, each one exhibiting progressive reduction.
2. Although the stamen vasculature is similar throughout the genus, stamen insertion shows migration from the base to the apex of the corolla and may be correlated with corolla venation.
3. The stigma shows a progressive reduction from the 3-cleft condition to one of entirety. This may be correlated with reduction in corolla vasculature.

4. The developmental trend in the capsule proceeds in two directions from a 3-locular, many-seeded, coriaceous structure. One direction has ended in a uni-locular, 1-seeded, chartaceous envelope having basal circumscissile dehiscence, while the other direction has terminated in indehiscent, thin-walled, several-seeded capsules. Correlation with corolla venation is less evident than elsewhere.

5. Vessel anatomy shows primitive vessels in species of little specialization.

6. Specialization in habitat is correlated with reduction in corolla venation, stigma lobation and staminal insertion.

7. Two sections of the genus, based upon morphological and ecological features, are accepted.

Division of Agronomy Herbarium,
University of California, Davis

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CHROMOSOME NUMBERS IN SILENE (CARYOPHYLLACEAE): I.

A. R. KRUCKEBERG¹

The genus *Silene* is represented in North America by fifty-four species, nine of which are introduced (Hitchcock and Maguire, 1947). All of the native perennial species, forty-two in number, are to be included in a current study of species interfertility and evolutionary relationships in the genus. In the course of this study, nineteen species of *Silene* and one of the closely related genus, *Lychnis*, have been examined cytologically. A summary of chromosome numbers (Table 1), camera lucida drawings of chromosome complements (figs. 1-28) and data on the cytological behavior of certain species and on the geographical source of the collected material are presented here.

The chromosome numbers were obtained primarily from acetic squash preparations of microsporocytes. Intact flower buds were fixed in three parts 95 per cent ethyl alcohol to one part glacial acetic acid and the anthers thus fixed squashed in acetocarmine. In cases where only pistillate plants of *Silene menziesii* Hook. were available, chromosome counts were made from aceto-orcein squashes of root tips or vegetative buds.

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TABLE 1. DIPLOID CHROMOSOME NUMBERS IN *SILENE*

		2n Chromosome Number	Number of Collections
<i>S. bridgesii</i> Rohrb.		48	1
<i>S. californica</i> Durand.	Tetraploid	48	3
	Octoploid	96	1
<i>S. campanulata</i> Wats.		48	2
<i>S. douglasii</i> Hook.		48	6
<i>S. hookeri</i> Nutt.		72	4
<i>S. laciniata</i> Cav.		96	3
<i>S. menziesii</i> Hook.	Diploid	24	1
	Tetraploid	48	11
<i>S. nuda</i> (Wats.) H. & M.		48	1
<i>S. oraria</i> Peck		48	1
<i>S. oregana</i> Wats.		48	1
<i>S. parishii</i> Wats.		48	1
<i>S. parryi</i> (Wats.) H. & M.	Tetraploid	48	4
	Octoploid	96	4
<i>S. sargentii</i> Wats.		48	2
<i>S. scouleri</i> Hook.	Tetraploid	48	2
	Octoploid	96	2
<i>S. scouleri</i> subsp. <i>grandis</i> (Eastw.) H. & M.		48	1
<i>S. scouleri</i> subsp. <i>pringlei</i> (Wats.) H. & M.		60	2
<i>S. seeleyi</i> Mort. & Thoms.		24	1
<i>S. stellata</i> (L.) Ait.		48	1
<i>S. verecunda</i> Wats. subsp. <i>platyota</i> (Wats.) H. & M.		48	2
<i>S. virginica</i> L.		48	2
<i>Lychnis drummondii</i> (Hook.) Wats.		48	1

The materials used were collected in the field or were taken from plants grown in the greenhouse from seed or from caudices collected in the wild. The camera lucida drawings were made at $\times 3300$ and reduced to $\times 825$.

CYTOLOGICAL OBSERVATIONS

The basic haploid number in *Silene* is 12 (Blackburn, 1928). Although none of the species from North America reported on here (Table 1) shows any deviation from that basic complement, it will be seen that the majority of them are polyploid derivatives of that number. Thus one species is diploid (*S. seeleyi* Mort. and Thoms.), one is diploid and tetraploid (*S. menziesii* Hook.), thirteen are tetraploid (see Table 1), one is tetraploid, pentaploid, and octoploid (the *S. scouleri* Hook. complex), two are tetraploid and octoploid [*S. californica* Dur. and *S. parryi* (Wats.) H. & M.], one is hexaploid (*S. hookeri* Nutt.), and one is octoploid (*S. laciniata* Cav.). This array of polyploids contrasts significantly with the European species for which chromosome numbers are available. In the most extensive listing of chromosome numbers in *Silene*, Blackburn (1928) reported on over forty Eurasian species, all but two of which were diploid. She listed under *Melandrium*, three North American species, *S. virginica* L., *S. pensylvanica* Michx., and *S. californica* Dur., all tetraploid ($2n = 48$).

The present work confirms Blackburn's count for *S. virginica* and for *S. californica*. However, one collection of the latter species was octoploid ($2n = 96$). The chromosome numbers of thirteen other European species, all diploid ($2n = 24$), were reported on by D. Löve (1942).

The author found that diakinesis was the most favorable stage for making chromosome counts (figs. 1-28). Normal chromosome pairing occurred regularly at diakinesis or at metaphase I in the diploids, as well as in the tetraploids, hexaploids, and octoploids. Irregularities during microsporogenesis were observed in only one species, *Silene scouleri* Hook. subsp. *pringlei* (Wats.) H. & M. In the two collections of this taxon studied, both of which came from Pima County, Arizona, the chromosome number at diakinesis (figs. 14 and 15) was somewhat variable, according to the number of univalents and bivalents present. Usually the number of univalents was 12 ± 2 and the number of bivalents, 24 ± 1 . From observations on chromosome pairing in several diakinesis figures, it appears that *S. scouleri* subsp. *pringlei* would have a somatic chromosome number of 60, thus making it a pentaploid. In both collections of subsp. *pringlei*, lagging univalents were to be seen at first and second telophases (figs. 16 and 17); as well, anaphase bridges were frequently observed. By the microspore stage, a large number of the quartets contained one to several micronuclei (Table 2 and figs. 18 and 19). Observations on pollen stained with cotton blue in lactophenol revealed 50 — 80 per cent empty pollen grains in these two collections. As yet the effects of this irregular meiotic behavior on seed production of subsp. *pringlei* in its native habitat is not known. However, in the greenhouse it does produce viable seed from selfed flowers; it has not yet been possible to study these seedlings cytologically. Further study will be made in an attempt to discover the cause of this irregularity and its extent throughout the range of *S. scouleri* subsp. *pringlei*.

GEOGRAPHICAL DISTRIBUTION

The geographical distribution of the colonies on which chromosome counts were made is given in the following list. Collections mentioned are represented by dried specimens on file in the University of Washington Herbarium.

SILENE BRIDGESII Rohrb. ($2n = 48$).

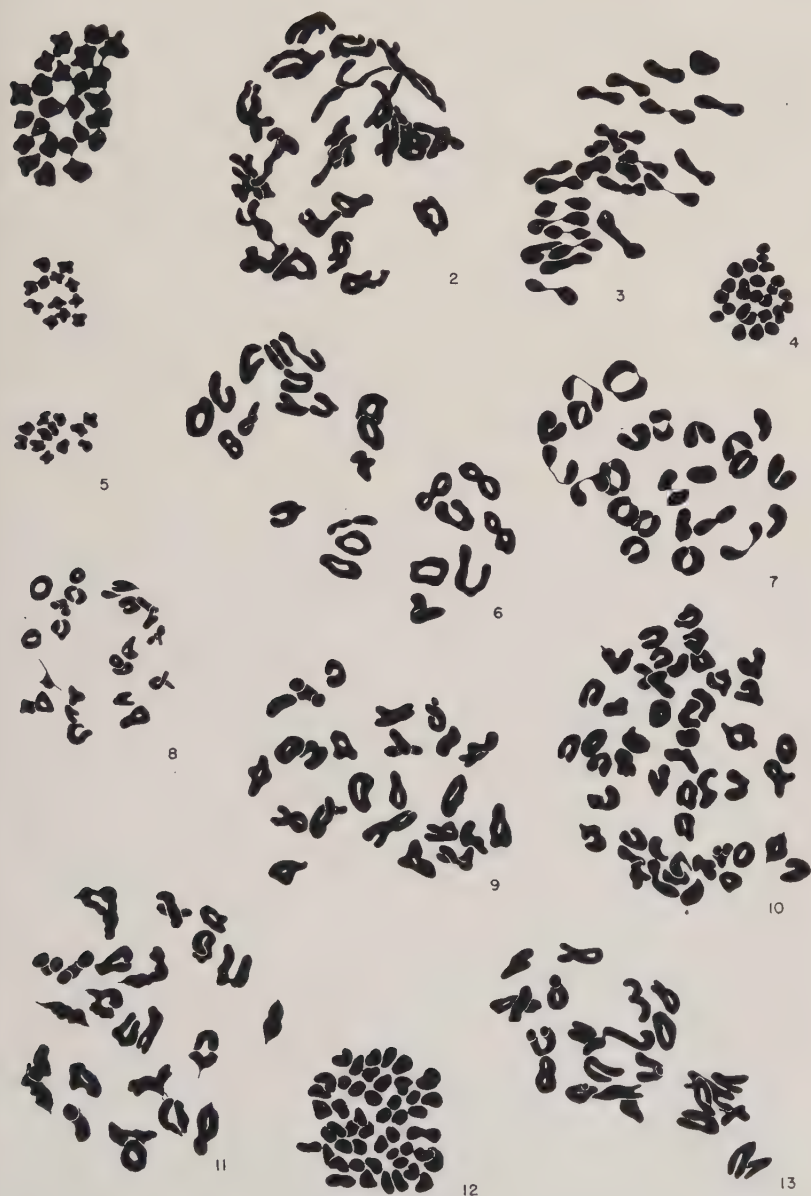
CALIFORNIA. Tuolumne County: 10 miles east of Big Oak Flat, *Hitchcock* 19630.

SILENE CALIFORNICA Durand. Tetraploid ($2n = 48$).

CALIFORNIA. Butte County: 12.7 miles northeast of Chico, *Bell*. Fresno County: 2 miles northeast of Auberry, *Quibell*. Mendocino County: Along Albion-Comptche road, north of Albion River, $\frac{3}{4}$ mile east of State Highway 1, *McMillan*.

SILENE CALIFORNICA Durand. Octoploid ($2n = 96$).

CALIFORNIA. Mendocino County: Ukiah (garden culture), *Purdy*.



FIGS. 1-13. Chromosomes of *Silene* microsporocytes, ca. $\times 825$. FIG. 1. *S. bridgesii*, I M (Hitchcock). FIG. 2. *S. campanulata*, Diak. (Kruckeberg 2714). FIG. 3. *S. douglasii*, I M (Kruckeberg 2078). FIG. 4. *S. menziesii*, I M (Kruckeberg 2752, Tetraploid). FIG. 5. *S. menziesii*, I T (Kruckeberg 2851, Diploid). FIG. 6. *S. nuda*, Diak. (Kruckeberg 2893). FIG. 7. *S. oraria*, Diak. (Hitchcock 20037). FIG. 8. *S. oregana*, Diak. (Kruckeberg 2458). FIG. 9. *S. parryi*, Diak. (Kruckeberg 3086, Tetraploid). FIG. 10. *S. parryi*, Diak. (Kruckeberg 2753, Octoploid). FIG. 11. *S. parishii*, Diak. (Snow 23). FIG. 12. *S. scouleri*, I M (Kruckeberg 3176, Octoploid). FIG. 13. *S. scouleri* subsp. *grandis*, Diak. (Hoffman, Tetraploid).

TABLE 2. NUMBER OF MICRONUCLEI IN POLLEN QUARTETS OF
SILENE SCOUERI SUBSP. PRINGLEI

Collection*	Number of micronuclei in quartets					Sporads with less than 4 microspores
	None†	one	two	three	four	
K. F. Parker	150	73	27	10	3	5
V. Grant	139	55	13	0	1	40

* See text for locality data.

† Many pollen grains of "none" class contained chromosomes excluded from nucleus.

SILENE CAMPANULATA Wats. ($2n = 48$).

OREGON. Jackson County: Along Palmer Ridge at Palmer Creek trail, Applegate-Ruch loop road, *Kruckeberg* 2714. Lane County: Wooded hillside overlooking Arm-itage Bridge and Mackenzie River, 6 miles northeast of Eugene, *Kruckeberg* 2916.

SILENE DOUGLASII Hook. ($2n = 48$).

NEVADA. Douglas County: $\frac{1}{4}$ -mile east of Spooner's Summit on U. S. Highway 50, *Kruckeberg* 2888.

OREGON. Deschutes County: In juniper-ponderosa pine, 5 miles southeast of junction, U. S. highways 20 and 28, between Tumalo and Sisters, *Kruckeberg* 2078.

WASHINGTON. Clallam County: Ridge trail between Mount Angeles and Hurricane Ridge, *Kruckeberg* 2794. Kittitas County: Lion Rock Lookout, eastern Wenatchee Mountains, *Kruckeberg* 3080; $\frac{1}{8}$ -mile southeast of Liberty Guard Station, Swauk Creek Canyon, *Kruckeberg* 3095. Spokane County: Along Brooks Road, 15 miles west of Spokane and 2 miles north of U. S. Highway 2, *Kruckeberg* 2811.

SILENE HOOKERI Nutt. ($2n = 72$).

OREGON. Douglas County: 2 miles east of Camas Valley on State Highway 42, *Kruckeberg* 3312. Jackson County: Thompson Creek road, below Guard Station, *Kruckeberg* 2712. Josephine County: Whiskey Creek, 3 miles west of Obrien, *Kruckeberg* 2907. Polk County: 3 miles northwest of Dallas on State Highway 22, *Kruckeberg* 2656, 3309.

SILENE LACINIATA Cav. ($2n = 48$).

CALIFORNIA. Los Angeles County: Cobal Canyon, San Gabriel Mountains, *Grant* 16119; near Whittier, *Thompson* 1431. Santa Barbara County: Laurel Canyon, *Stebbins* (August 7, 1951).

SILENE MENZIESII Hook., Diploid ($2n = 24$).

IDAHO. Blaine County: Trail Creek Forest Camp, 2 miles east of Sun Valley, *Kruckeberg* 2851.

SILENE MENZIESII Hook. Tetraploid ($2n = 48$).

OREGON. Klamath County: 5 miles west of Sprague River junction, *Hitchcock* 19498. Lake County: 25 miles northwest of Lakeview, *Hitchcock* 19489.

WASHINGTON. Chelan County: Upper Nigger Creek Trail, $\frac{1}{8}$ -mile above Horse Pasture, Wenatchee Mountains, *Kruckeberg* 2752; near fork of Nigger Creek and King Creek trails, Wenatchee Mountains, *Kruckeberg* 2764. Spokane County: Just north of Dartford, near summit of grade on U. S. Highway 395, 17 miles north of Spokane, *Kruckeberg* 2823.

IDAHO. Nez Perce County: Lewiston Hill, 6 miles north of Lewiston, *Hitchcock* 19437. Lewis County: Lawyer Creek camp between Craigmont and Ferdinand on U. S. Highway 95, *Kruckeberg* 2830. Valley County: 7 miles west of McCall, *Kruckeberg* 2843; granitic pine hills between Cascade and Smith Ferry, North Fork of Payette River, *Kruckeberg* 2847.



FIGS. 14-25. Chromosomes of *Silene* microsporocytes, ca. $\times 825$. FIG. 14. *S. scouleri* subsp. *pringlei*, Diak. (Grant 16134, Pentaploid). FIG. 15. *S. scouleri* subsp. *pringlei*, Diak. (Parker, Pentaploid). FIG. 16. *S. s. pringlei*, I T, with lagging univalents (Parker). FIG. 17. *S. s. pringlei*, II T, with lagging chromosomes (Parker). FIGS. 18, 19. *S. s. pringlei*, sporad stage; abnormal pollen grains and micronuclei (Parker). FIG. 20. *S. seeleyi*, I M (Kruckeberg 2751). FIG. 21. *S. stellata*, Diak. (Lemmon). FIG. 22. *S. verecunda*, I M (Snow 22). FIG. 23. *S. virginica*, I M (Lemmon). FIG. 24. *S. sargentii*, Diak. (Kruckeberg 2889). FIG. 25. *Lychnis drummondii*, Diak. (Kruckeberg 2874).

UTAH. Cache County: 18 miles up Logan Canyon, *Holmgren* (September 25, 1953).
San Pete County: Above Baldy Ranger Station, on Skyline Drive, Wasatch Plateau, *Kruckeberg* 2873.

SILENE NUDA (Wats.) H. & M. ($2n = 48$).

CALIFORNIA. Sierra County: Just north of summit between turnoff to Calpine Lookout and Graeagle, State Highway 89, *Kruckeberg* 2893.

SILENE ORARIA Peck ($2n = 48$).

OREGON. Tillamook County: On bluffs above the sea at mouth of Salmon River, Cascade Head Forest Experiment Station, *Hitchcock* 20037.

SILENE OREGANA Wats. ($2n = 48$).

OREGON. Wallowa County: Sacajawea Camp near Hat Point, *Kruckeberg* 2458.

SILENE PARISHII Wats. ($2n = 48$).

CALIFORNIA. San Bernardino County: Grout Creek Bridge, Bear Valley, *Snow* 23.

SILENE PARRYI (Wats.) H. & M. Tetraploid ($2n = 48$).

WASHINGTON. Chelan County: Mount Lilian (Table Mountain area), eastern Wenatchee Mountains, *Kruckeberg* 3049; Mission Peak (Table Mountain area), eastern Wenatchee Mountains, *Kruckeberg* 3086; Naneum Meadows, 2 miles east of turnoff to Lion Rock Lookout, eastern Wenatchee Mountains, *Kruckeberg* 3248; slopes of Mission Peak, eastern Wenatchee Mountains, *Phillips* (September, 1953).

SILENE PARRYI (Wats.) H. & M. Octoploid ($2n = 96$).

WASHINGTON. Chelan County: $\frac{1}{8}$ -mile above Horse Pasture, upper Nigger Creek trail, western Wenatchee Mountains, *Kruckeberg* 2753; at 5-mile marker on upper Nigger Creek Trail, western Wenatchee Mountains, *Kruckeberg* 2762. Kittitas County: DeRoux Forest Camp, North Fork Teanaway River, western Wenatchee Mountains, *Kruckeberg* 2673; Fish Lake, Upper Cle Elum River, *Kruckeberg* 2961.

SILENE SARGENTII Wats. ($2n = 48$).

CALIFORNIA. Lassen County: Lake Helen, Lassen National Park, *Kruckeberg* 2899.

SILENE SCOULERI Hook. Tetraploid ($2n = 48$).

WASHINGTON. Pierce County: Tacoma prairies between Spanaway and Roy, *Kruckeberg* 2744. Spokane County: Philleo Lake, 6 miles west of Spangle, *Kruckeberg* 2828.

SILENE SCOULERI Hook. Octoploid ($2n = 96$).

OREGON. Wallowa County: West side of east lateral moraine, Wallowa Lake, *Kruckeberg* 3176.

IDAHO. Nez Perce County: Summit of Winchester Grade, 25 miles south of Lewiston, on U. S. Highway 95, *Kruckeberg* 3179.

SILENE SCOULERI Hook. subsp. *GRANDIS* (Eastw.) H. & M. ($2n = 48$).

CALIFORNIA. Sonoma County: Ocean bluffs at Wright's Beach, *Hoffman* (September 7, 1951).

SILENE SCOULERI Hook. subsp. *PRINGLEI* (Wats.) H. & M. ($2n = 60$).

ARIZONA. Pima County: Mount Lemmon, Santa Catalina Mountains, *Grant* 16134 (September 15, 1951); Mount Lemmon, Santa Catalina Mountains, *Parker* (September 21, 1952).

SILENE SEELEYI Morton & Thompson ($2n = 24$).

WASHINGTON. Chelan County: Basalt cliffs, $\frac{1}{8}$ -mile above Horse Pasture, upper Nigger Creek trail, western Wenatchee Mountains, *Kruckeberg* 2751.



FIGS. 26-28. Chromosomes of *Silene* microsporocytes, ca. $\times 825$. FIG. 26. *S. californica*, Diak. (Bell). FIG. 27. *S. hookeri*, Diak. (Kruckeberg 2696). FIG. 28. *S. laciniata*, Diak. (Stebbins).

SILENE STELLATA (L.) Ait. ($2n = 48$).

GEORGIA. Cobb County: Marietta, Lemmon.

SILENE VERECUNDA Wats. subsp. *PLATYOTA* (Wats.) H. & M. ($2n = 48$).

CALIFORNIA. Riverside County: Hall Canyon, San Jacinto Mountains, Kamb; San Bernardino County: Hanna Flats Forest Camp, Bear Valley, Snow 22.

SILENE VIRGINICA L. ($2n = 48$).

GEORGIA. Cobb County: Marietta, Lemmon.

NORTH CAROLINA. Buncombe County: Asheville, Bell.

LYCHNIS DRUMMONDII (Hook.) Wats. ($2n = 48$).

UTAH. San Pete County: Spruce meadows above Baldy Ranger Station, Skyline Drive, Wasatch Plateau, Kruckeberg 2874.

Although *S. parryi* (Wats.) H. & M. is a widespread species in the Northwest, to date study material has been limited to collections from the Wenatchee Mountains in central Washington. In this small geographic area of approximately 300 square miles, two distinct chromosomal races have been observed. The octoploid form predominates in the western Wenatchees, an area extending from the Cascade Crest to Blewett Pass and Swauk Creek. This western half of the Wenatchee Mountain spur is predominantly an igneous formation, acid (granitic) and ultrabasic (peridotites and serpentine) forming the chief rock types. In this area the octoploid form of *S. parryi* occurs primarily on the ultra-basic igneous formations at from 5,000 to 8,000 feet elevation; in contrast, the tetraploid counterpart has been found on the high basaltic plateau of the Table Mountain-Mission Peak areas which constitute the eastern end of the Wenatchee Mountain spur.

Another species in which there is more than one ploidy level is *S. scouleri* Hook. The three tetraploid collections are widely separated geographically and include the robust coastal subsp. *grandis* (Eastw.) H. & M. from California. The two from Washington are probably referable to subsp. *typica* H. & M., although the collection from the Tacoma Prairies is suggestive of the stature and flower color of subsp. *grandis*. The octoploid forms of subsp. *typica* were from ecologically similar and geographically adjacent areas, separated from one another by the Snake River Canyon. The third subspecies of *S. scouleri*—subsp. *pringlei*—the pentaploid with $2n = 60$ has already been referred to in connection with its irregular meiotic behavior. It is a well-defined taxon with more remote affinities with *S. scouleri* than any others of the subspecies in this polymorphic species. Interfertility studies, now in progress, involving hybridizations between subsp. *pringlei* and subsp. *typica*, as well as among other related taxa, may clarify the systematic position of this puzzling entity.

The present observations on chromosome number in North American species of *Silene* have disclosed the existence of a polyploid seriation ranging from $2n = 24$ to $2n = 96$. When more cytological data as well as observations on interfertility are available for the balance of the North American species, it is hoped that inferences of relationship within the genus may be drawn with greater certainty than they have been in the past.

Department of Botany,
University of Washington, Seattle 5.

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A DEPHLOGISTICATED SPECIES CONCEPT

J. F. DAVIDSON

Some two hundred fifty years ago in the field of chemistry there was considerable discussion as to the reality, the nature and attributes of "phlogiston", the essence of combustion. For many years, there has been no question as to the reality of this element which produced fire. Since many substances were combustible, it was obvious to the early workers that these materials contained phlogiston. Once such combustibles had been burned, thereby removing the phlogiston, they would no longer burn. They were dephlogisticated.

Acceptance of the phlogiston theory, however, brought problems. For example, charcoal was burned completely and must therefore have been

pure phlogiston. However, sulphur was also completely consumed on burning and must also be pure phlogiston. Yet sulphur and charcoal were obviously not the same substance. Then, too, both charcoal and sulphur could be weighed, and if the end products of combustion were collected and weighed, these end products weighed more than the original materials. Since, presumably, phlogiston had been removed, then phlogiston must have a negative weight. Yet the pure phlogiston, in either charcoal or sulphur, had had a positive weight!

Such arguments, which may appear absurd to us now, finally succumbed to a re-evaluation of the facts of combustion.

The term *species* today is in a somewhat similar position to that of phlogiston two and a half centuries ago. There are today many discussions concerning species, their delimitation, attributes and definition, and these discussions often savour faintly of the arguments in favor of either charcoal or sulphur being pure phlogiston. The reality of the species as a biological or physical unit is probably only as valid as the reality of phlogiston as a chemical unit or element. Perhaps it is time that we, like the chemists of the past, re-examine the factual bases upon which our concepts rest. Such a re-examination is attempted here.

It is not our intention to discard the term *species*, nor yet to offer another definition to the multitude already in existence. It is instead, to attempt to reach some common ground of agreement based upon a foundation of fact. As we are now finding, without such common agreement, the term species will be vague and meaningless and will lead ultimately to confusion.

As we examine the various definitions of species which have been proposed, the sole feature that appears to be common to all is the statement that species are composed of individuals which possess certain common characteristics. The nature of these common characteristics varies with the different definitions. It should therefore be possible to start at this level of agreement in the development of our thesis, namely, that each species is composed of a number of individuals.

In nature, the question of individuality may arise in such forms as *Volvox*, where the problem concerns a choice between considering the sphere as a colony of individual cells or as a single individual organism. The question may also arise in the lichens, where the problem concerns the choice between dealing with the lichen as a single organism or as a symbiotic relationship between an alga and a fungus. Normally, however, in the higher plants, despite the common occurrence of symbionts and parasites, there is no question as to the individuality of a plant. This recognition of individuality is an inherent part of the various species definitions, so that we are not here implying anything novel. For this reason, we may accept the occurrence of individual plants as the basis for taxonomy and classification in this group.

Since classification implies the sorting into classes, any classification of plants must attempt to separate the total mass of plants into groups. This total mass of plants includes all plants of all time, living and fossil, as well as those which have left no trace of their existence. If we had access to this total mass of plants, and if we accept the theory of evolution, it is obvious that we would be faced with a single continuum. It is also obvious that any classification of such a continuum would have to be based upon arbitrary standards, since at some point we would be forced to separate parent from offspring as belonging to different groups.

As classifiers, we should therefore be extremely thankful for the occurrence of extinction, because in dealing with contemporary plants, the extinction of the intervening individuals creates a gap in the continuum. When we attempt to portray the conditions found in nature in our system of classification, we utilize these gaps in the continuum as convenient places to draw a line of separation between groups of individuals. In palaeontology as well, the absence of certain intermediate fossil types also serves as a convenient gap for classification purposes.

Extinction is not a phenomenon of the past alone, but is also in operation today. As this is written, in some plant fertilization is occurring which will result in an embryo predestined for death or extinction before completion of its life cycle due to the physiology of the plant embryo being inadequate at some phase of its ontogeny. This inadequacy of the physiology is due in turn to the inadequacy of the genic complement of the zygote for the environment in which the embryo or seedling finds itself. As a corollary, each plant which lives to complete its life cycle obviously possesses a genic constitution adequate for the environment in which it lives. The environment selects for survival only those individuals with favorable gene combinations, and dooms the vast majority of the offspring to perish. If this were not true, we would soon be overpopulated with a given type of plant. Selection by the environment eliminates certain gene combinations and thereby produces discontinuities. These discontinuities involve a basic discontinuity in the total gene constitution.

Since it would be quite irrational to attempt to determine the total gene constitution of all individuals, we attempt to approximate this objective by determining the discontinuities in the distribution of characters which are controlled by genes. Since genes apparently control the physiology of the individual, and through the physiology both the morphology and the reactions of the individual to the environment, it would appear that discontinuity in the distribution of any character would serve as an indication of genic discontinuity.

It is possible to find in nature chromosomal translocations and inversions which produce genetic discontinuity. That is, individuals carrying these chromosomal aberrations show a great reduction in fertility when crossed with individuals carrying the normal chromosome complement. This may occur, however, when the total gene constitutions of the interbreeding individuals are practically identical. Hence such intersterility

cannot be used as an infallible measure of genic dissimilarity. Although individuals with mutually exclusive gene patterns are also intersterile, there is absolutely no assurance that a mere reduction in fertility is accompanied by a corresponding diversity of genic constitution. Intersterility in itself is an indication of a difference of physiology of the gametes involved, and may be of major or minor nature. It is of comparable importance to other physiological differences, such as those which may concern environmental relations.

If we include geographical and temporal distribution, discontinuities are of universal occurrence in nature, since no two individuals can occupy the same space at the same time. We are capable of bridging many of these discontinuities mentally. In fact, we frequently do so unconsciously, and then have a difficult time in appreciating the existence of the discontinuity. For example, when we encounter a patch of violets in the woods, we are apt to think of it in terms of a unit. We mentally group the similar individuals together into a single unit, despite the fact that the only units present are the individual plants. Their geographical proximity is purely relative to their proximity to each other as compared with the distance of the members to plants in other patches. Even the phylogenetic continuum mentioned earlier is more apparent than real since the offspring of sexually-reproducing parents is not the same organism as either parent. Thus the phylogenetic lineage is a series of descendant individuals which we see as a continuum only through our mental processes.

The tendency to speak and think in terms of attributes of a group of individuals, apart from the attributes of the individual components, is another example of mental aggregation or mental perception. As an example, one can readily see the triangle formed by setting up ten pins in a bowling alley, yet the triangle is not an attribute of any single pin, but rather of the whole group of pins. The triangle in this case is purely mental. *We* mentally construct three lines bounding the pins and we mentally produce them until they meet to form the triangle. In the same manner, we tend to bound a "grove" of trees, by drawing a mental line around the outermost trees. When the distance between two groves approximates the distance between the trees within the groves, then the process of drawing the boundaries becomes more difficult. Basically, of course, there is no doubt that there is a given number of trees, each in its own location. Whether they form one grove or two can be debated indefinitely and to no purpose.

Thus it would appear that all aggregation of individuals into groups is therefore a process of lesser or greater mental difficulty. In many cases, where a number of individual plants possess a combination of many characters which is unknown in other plant groups, the aggregation into a unit is mentally very simple. The fact that the combination of characters is unknown elsewhere implies discontinuity in the distribution of these characters. The greater the number of these characters, the easier is our mental aggregation of the individuals possessing them. We have, on the

other hand, groups of plants in which there are few common characters, and here the mental process of aggregation becomes increasingly difficult as the number of common characters is reduced.

It is logical, therefore, that as we progress through the aggregation process, from parent and offspring, through population, form, variety, species, genus, family, order, and class, there will be progressively fewer common characters held by all the component individuals, and hence the aggregation process will become increasingly difficult.

As one might expect, there is a great range in the magnitude of discontinuities between groups of individuals. On the one hand, we have the situation which exists in the maidenhair tree (*Ginkgo biloba*), in which the plants are so unlike anything else that they constitute a distinct order, yet they are at the same time so much alike that all the individuals are commonly referred to one species. On the other hand, we have the situation which exists in the genus *Salix*, the willows. Here, many of the species of the northwestern United States are all capable of interbreeding to produce fertile offspring. If we wish to argue that species have an objective reality, we may select examples such as *Ginkgo*. If we wish to argue that species do not exist in nature at all, we may select such examples as the willows. A true understanding of the situation in nature, however, must embrace both of these extreme cases.

There is sufficient discontinuity apparent in nature to retain the term "species" as a convenient designation, provided that the user and listener is each cognizant of the significance of its use. While the individuals which comprise the species are aggregated on the basis of their common characters, it must be recognized that these individuals can be assumed to be alike only in these determined respects. In any other character, variation should be expected until constancy is demonstrated. We must be forever conscious of the fact that a species is not a homogeneous group of identical individuals, but, on the contrary, within a species variation is more common than constancy.

Since the list of characters common to the individuals of a species is compiled by various workers, and since these workers usually select different samples, the lists of common characters are necessarily subjective. Also, since the characters of the species are nothing more or less than the list of common characters, it would appear that the species itself is merely a mental aggregation of the individuals bearing these characters.

This does not deny the existence of species, but indicates that they are mental units rather than biological units. The biological units are the individuals and these functioning individuals are interrelated through their phylogenetic lineages. We have a hierarchy of categories set up by international agreement through which we may express our concepts of these relationships. The more minor the category selected to embrace two individuals, the closer is the suggested relationship. Thus two individuals in the same *forma* are presumed to be more closely related than they would be if placed in different *forma* in the same variety; and the

latter would be more closely related than if they were placed in different varieties, or different species.

The question of paramount importance is "How are these individuals related," not "To what category should each be assigned?" If an analogy might be used, we could consider a river system. It matters little whether the tributaries are called creeks, runs, streams, rills, brooks, or rivers. The important aspect concerns their location, depth, breadth, and rate of flow. So with our plants, the "species problem" concerns not so much what constitutes a species, but rather, what are the attributes of the individuals included in each species. As our knowledge of these attributes grows, apparently conflicting evidence will tend to disappear, since there can be no conflict in truth, and a more accurate portrayal of relationships will be possible.

Department of Botany,
University of Nebraska, Lincoln

APACHE PINE AND ITS RELATIONSHIP TO PONDEROSA PINE

N. T. MIROV¹

Righter and Duffield (1951) described a hybrid obtained by crossing ponderosa pine (*Pinus ponderosa* Laws.) and Apache pine (*P. latifolia* Sarg.). The hybrid possessed several advantageous characters, such as a long taproot and rapidity of growth. It appears to be interesting to inquire into the taxonomic status of the parents because their relationship is far from being settled.

Some botanists (Shaw, 1914, p. 66) consider the Apache pine of southwestern United States and Mexico merely a variety of ponderosa pine. From their point of view the hybrid *P. latifolia* \times *P. ponderosa* is, then, the product of an intraspecific hybridization, i.e. hybridization of two varieties of the same species. Others (Sudworth, 1917, pp. 33-35) believe that Apache and ponderosa pines are distinct species; thus the hybrid should be considered, by those who share this opinion, as the result of a distant (interspecific) hybridization.

Ponderosa pine is a generally recognized species. The several varieties which have been described under it (such as var. *scopulorum* Lemmon or var. *nigricans* Lemmon) are considered valid by some botanists, while others do not believe that these entities merit varietal status. (*Pinus Jeffreyi* Grev. & Balf., at one time regarded as a variety of *P. ponderosa*, is now considered a distinct species by most workers.)

¹ Physiologist, Institute of Forest Genetics, California Forest and Range Experiment Station, maintained by the Forest Service, U. S. Department of Agriculture, in cooperation with the University of California, Berkeley. The experimental work on which this paper is based was aided by a grant from the Rockefeller Foundation.

The status of Apache pine, however, is more complicated. Specimens of this pine have been described by various botanists as distinct species (*P. macrophylla* Engelm., 1887; *P. latifolia* Sarg., 1889; *P. apachea* Lemmon, 1894; *P. mayriana* Sudw., 1897). All these names signify that Apache pine may be entitled to the rank of a species. On the other hand, Shaw (1914) does not consider Apache pine as distinct from ponderosa pine and places these names in synonymy under *P. ponderosa*. (In the new Forest Service Check List . . . , Trees of the United States, Handbook 41, Wash., 1953, Apache Pine is listed as *P. engelmannii*.)

Herbarium specimens of *P. latifolia* and *P. ponderosa* are very similar in appearance. However, foresters and those botanists who are familiar with the two pines growing under natural conditions, are aware of many characters of Apache pine that are different from the characters of ponderosa pine. These characters are: long, lush-green foliage, deep taproot of seedlings, a seedling "grass stage" similar to that of *P. palustris* and (in lesser degree) of *P. montezumae*, red-brown color of bark scales, and others. It is on these bases that Apache pine was considered to be a distinct species by the early workers.

Recent biochemical investigations of ponderosa and Apache pines, conducted at the Institute of Forest Genetics, furnish additional information in regard to the botanical relationship of the two. It was found that all investigated varieties of ponderosa pine—from California, northern Idaho, the Black Hills of South Dakota, Colorado, Utah, and Arizona (Haagen-Smit et al., 1950; Iloff and Mirov, 1954, Mirov, 1951) may be characterized by the presence in their turpentine of large quantities of a terpene, delta-3-carene. This terpene may be thus considered as a specific character of ponderosa pine throughout its range. On the contrary, turpentine of Apache pine does not contain any delta-3-carene. Thus, taking into consideration its chemical characters, Apache pine should be classified as a distinct species and not as a variety of ponderosa pine.

Berkeley, California

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